

Poorly explored jewels of the tropics: Estimating diversity in non-pulmonate land snails of the family Helicinidae (Gastropoda: Neritopsina)*

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Abstract: Helicinids represent a family of tropical land snails with a distribution range limited to the subtropical and tropical zones of the New World, Australasia, and the Pacific. For an estimate of diversity in this poorly systematically revised group, the total number of described taxa was determined and used for calculations based on analyses of selected case studies with regard to the percentage of valid and new taxa.

Extensive bibliographic searches identified about 1,250 available names, regardless of rank, that were described from 1801 onward. Fifty-eight percent of the names represent New World taxa whose majority (63%) was created before 1880 while the intensive study in most of the Australasian and Pacific areas started much later with the bulk of taxa described between 1880–1930. An analysis of the distribution of the type localities and the times of descriptions allowed for identification of scarcely- and well-studied areas.

Eight potentially representative case studies of major revisions were compared with respect to changes in described versus “true” diversity. The geographic range covered Costa Rica, Cuba, Jamaica, Lesser Antilles, New Caledonia, northeast Australia, and the Hawaiian and Gambier Islands. In these studies approximately half of the available names were regarded as synonyms (range from 37 to 72%). On the other hand, 36 to 41% of the recognized diversity represented new species depending on whether a more lumping or splitting approach was considered, the latter simulated by simply counting subspecies as equal units of diversity. The amount of new taxa ranged from 2% (Cuba) to 90% (Gambier Islands). Under the assumption that six of the studies were representative throughout the area of distribution, worldwide diversity would range from 770 to 1,140 species or up to 1,400 species if the studies from the Australasian-Pacific area were realistic. Although obviously poorly studied, in comparison with an estimate for all continental molluscs of Mexico and Central America by Thompson (2011), helicinids would still be among the better documented snail families for this region.

The following aspects and their consequences are discussed as most significant drawbacks in the exploration of helicinids: questionable systematic concepts above species level; limited recognized differentiating characters and convergence; species complexes and last, massive habitat loss, increasingly fragmented distribution and extinction. Another practical aspect is the rather limited availability of wet preserved material.

Key words: systematics, alpha-taxonomy, research history, synonymy, distribution

This contribution aims to provide a realistic estimate on the diversity of the family Helicinidae. Helicinidae together with the closely related Proserpinidae and Proserpinellidae represent an independent evolutionary branch to a terrestrial mode of life that rarely conquered drier habitats. The main distribution of helicinids stretches throughout the tropics of the New World, Australasia, and the Pacific. They are absent in Africa and on the Indian subcontinent with a single species occurring on the Seychelles (Fig. 1). Among the families mentioned only helicinids underwent some spectacular radiations, e.g., the Stoastomatinae on Jamaica, and reached a recent diversity

comparable to some large pulmonate families. Clausiliidae, for example, a family that evolved the unique clausilium as closing device, comprise nearly 1,300 recent species (Nordsieck 2007) which might be about 1.5 times helicinid diversity.

A well-founded assessment of the diversity of helicinids would require a revision of all taxa described with current state-of-the-art methodology and sufficient sampling efforts in all regions of the distribution. In a group of organisms of no given economic or nutritional value, with its main distribution in tropical countries with a very limited local systematic workforce and which never seriously attracted the attention of

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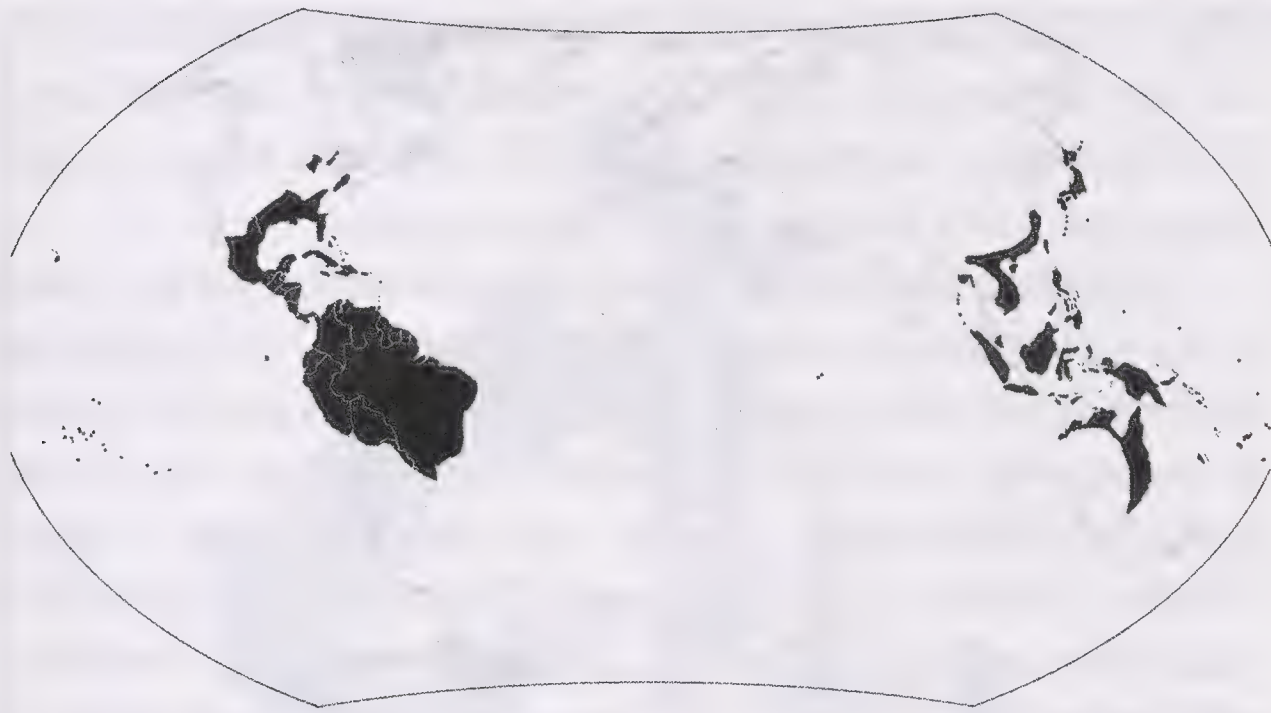


Figure 1. Distribution of the family Helicinidae (in black), partially generalized to political units disregarding habitat suitability, small islands enlarged as dots.

collectors or amateur scientists, this undertaking is unrealistic. Therefore, the current study explores the amount of divergence of theory to actual knowledge by analyzing the exploration of the family over time, by reviewing selected case studies and identifying well- and poorly-sampled areas. Furthermore, it will examine the specific difficulties in helicinid systematic research and the reasons for taxonomic confusion.

HISTORY OF HELICINID RESEARCH

The first helicinid was described in 1801 by Lamarck (*Helicina neritella* from Jamaica) relatively long after the introduction of the binomial nomenclature by Linnaeus (1758); that is probably due to the tropical distribution of the group. The major phase of species descriptions (Fig. 2) is linked to the scientific output of the German malacologist Louis Pfeiffer who took a strong interest in the family. He described

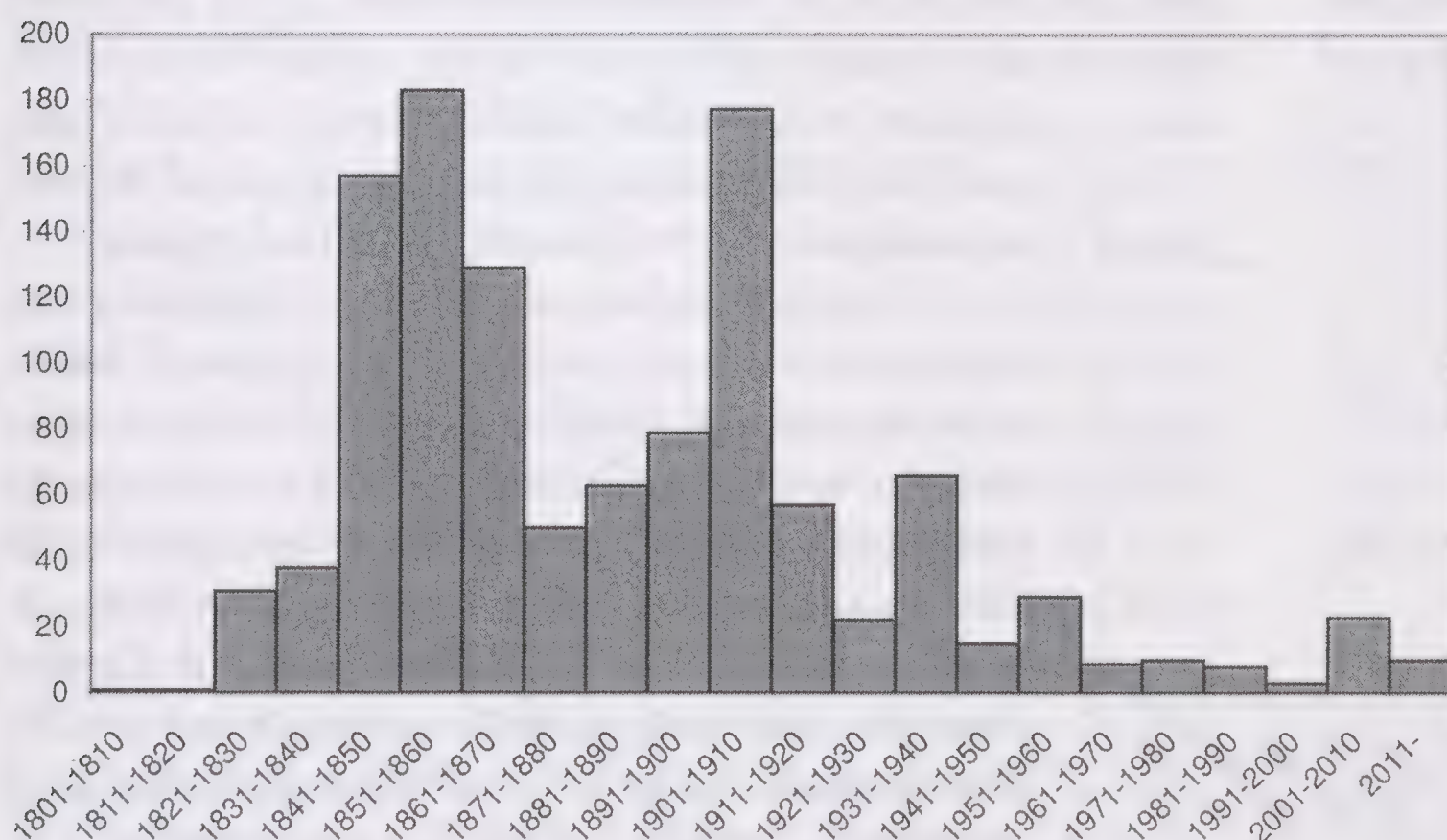


Figure 2. History of research—number of new helicinid taxa described per decade.

more than 170 helicinid taxa which is unsurpassed by any other author. In addition, Pfeiffer (1850–1853) wrote the first helicinid part of the famous *Martini and Chemnitz Systematisches Conchylien-Cabinet* and continued to provide detailed and updated species lists in the four volumes of the *Monographia Pneumonopomorum viventium* (Pfeiffer 1852, 1858, 1865, 1876). The helicinid chapters in the *Thesaurus conchyliorum* (Sowerby 1842, 1866) constitute the only other significant comprehensive publications of this period although short in text. The presentation in Reeve (1873) is mentioned for completeness, but added little information due to the rather poor quality of the drawings.

Species descriptions kept accumulating after Louis Pfeiffer's death in 1877 although at a lower rate and the new edition of the *Martini and Chemnitz Systematisches Conchylienkabinett* (Wagner 1907–1911) was the appropriate occasion for a new and the last comprehensive and illustrated presentation of the entire family. In the absence of an expert for the family, Kobelt motivated Antoni Józef Wagner—otherwise working on European land snails—to explore this exotic family (Richling 2005a). Wagner's monograph (1907–1911) and two pre-studies (Wagner 1905a, b) included another 135 new taxa entirely based on material studied in museum collections or gathered by exchange from other malacologists of his time. He recognized 529 species and subspecies, but overlooked another 137 taxa (Fulton 1915). Subsequently the description of new taxa basically slowed down in the 20th century: Pilsbry with new species from nearly the whole Neotropical range of distribution, Aguayo—often co-authored by Jaume—on Cuban material, and Neal (1934) in the revision of the Hawaiian helicinids were the most prolific authors of this period.

METHODS

For the search of helicinid taxa, in addition to the helicinid literature mentioned in the introduction, sources such as the *Zoological Record*, Sherborn (1922–1931), and Ruhoff (1980) were used. This compilation was complemented by the analysis of more than 500 primary and secondary publications.

In counts of taxa obvious misspellings or errors, homonymous *minor*, *major*, etc., and unavailable names were excluded. For subspecies, the nominal subspecies were included in the number of species and only additional subspecies were counted separately. For practical purposes of the present analysis, the geographic attribution of names was simplified to a single political unit in case of multiple type localities. Equally, it does not strictly follow the original description but was adjusted to the present knowledge, e.g.,

when a species was described with unknown or an erroneous origin, but can be localized now. The systematic arrangement follows Bouchet and Rocroi (2005).

The case studies explored were selected by the fulfillment of the following criteria: 1) approach on the level of a revision, 2) realization of extensive field work or study of significant collections, 3) study of type material, and 4) coverage of a meaningful political or geographical entity. In addition, a wide range of different specific circumstances and geographical coverage was included.

RESULTS AND DISCUSSION

Available names, geographic distribution, and time scale of explorations

The search for described taxa resulted in approximately 1,250 available names for recent Helicinidae regardless of their rank and nearly 30 names for Proserpinidae and Proserpinellidae *sensu* Thompson (1980, as Ceresidae). About 720 names (~ 58%) were created for New World helicinids including the Galapagos representatives that seem to be more closely related to the Pacific species (Wagner 1907–1911). Roughly 500 taxa (about 40%) cover the Australasian and Pacific helicinids. Only 23 taxa still lack a clear geographic attribution (unknown or too vague like “Pacific” or “South America”).

Although an extensive search of literature was performed it is likely that a few descriptions in local journals and little-used languages remain overlooked, but their number is assumed to be rather small. In a less intensive search for new marine taxa that was counterchecked a year later, Bouchet (2006) reported the insignificant amount of only 1.6% uncaptured names.

The major phases of exploration were highlighted in the research history. Typically, the description of species started slow, but along with growing settlements, trade, and further expeditions in the tropics a boom of discoveries followed

(Fig. 3). The curve shows two major points of deceleration, the first around the 1880's, that parallels the death of Louis Pfeiffer, and a second around 1930, before it enters a slow phase and more linear trend in recent years.

Although the rate of descriptions dropped, an approach to the saturation zone as it seemed towards the end of the last century is not yet apparent. The time between the two points of slowdown includes the major contributions by Ancey, Bartsch, Möllendorff, Pilsbry and the work by Wagner (1905a, b, 1907–1911). The “jump” between 1930 and 1940 is caused by a single paper, *i.e.*, the revision of the Hawaiian species by Neal (1934) including a high number of intraspecific taxa. More than 50% of all taxa were described by 1880, about 60% by the end of the 19th century, and more than 85% by 1930. For a further analysis in a geographical context, it seems helpful to differentiate roughly three intervals, 1800–1880, 1880–1930, and 1930–recent, to understand the time scale as well (Figs. 4 and 5).

In the New World the highest number of taxa concentrates on the Greater Antilles with Cuba only slightly ahead of Jamaica (Fig. 4). However, more than half of the Jamaican taxa are constituted by the Stoastomatinae that underwent a major radiation only on this island. Therefore, comparable named helicinid diversity on Jamaica lies in the same range as Hispaniola or the entire area of Mexico. Potential diversity reflected in taxa described shows higher numbers on islands with usually endemic species whereas diversity is lower on the mainland of Central and northern South America where described taxa are “randomly” split up in different political units although species distributions cross these borders. The distribution of the latter taxa is, therefore, superimposed by effects of research intensity and the onset of discovery. Countries explored earlier will have more type localities than later investigated areas which is clearly shown for *e.g.*, Nicaragua, Panama, Honduras with very few taxa and most explicitly Belize with no taxon described from its area. But according to personal observations in the collection of the Florida Museum of Natural History, Gainesville (unpubl. data) at least seven helicinid species occur in Honduras while Thompson (2011) only extracted records of two species from literature reviewed by him.

The West Indies—except for Hispaniola and the Bahamas—with neighboring areas of South America and the suitable parts of North America and the northern Central America received the earliest attention by helicinid authors. In fact, the three earliest described species originate from Jamaica and the United States. Southern Central America, vast parts of South America and smaller islands were studied much later and obviously constitute a major source for new species, *e.g.*, Costa Rica (Richling 2001, 2004a) and Colombia (Hausdorf 2006).

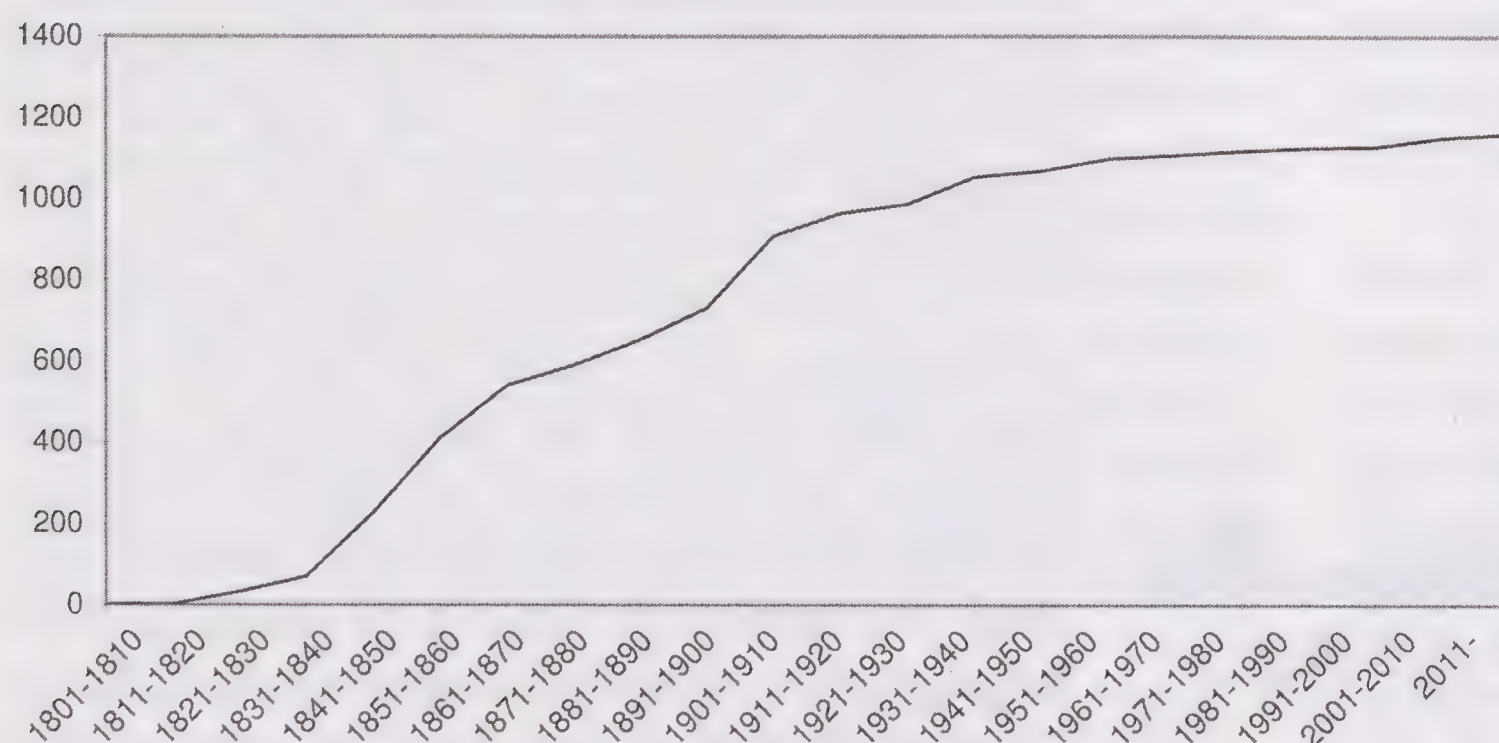


Figure 3. Accumulation curve of newly described helicinid taxa over time.

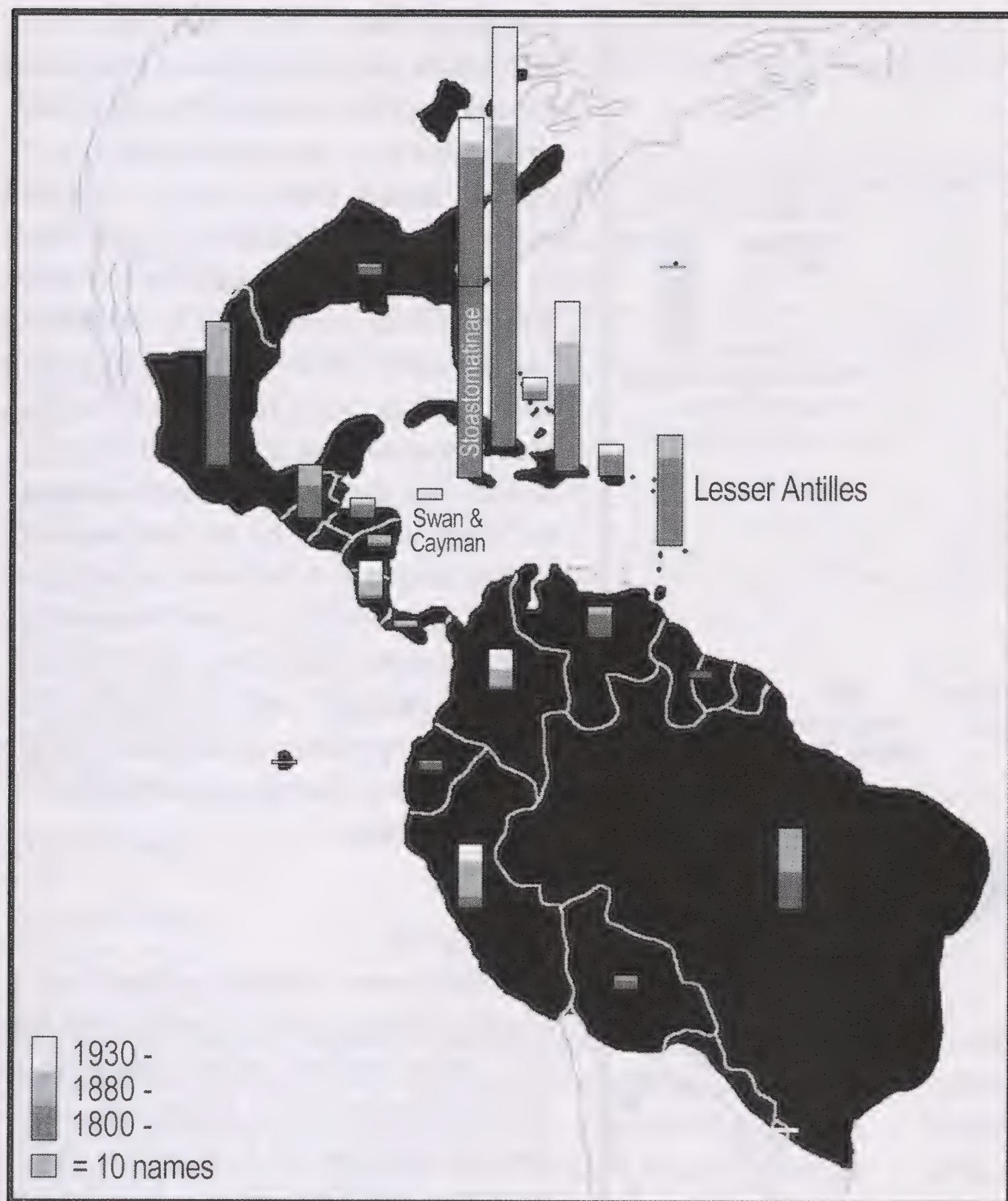


Figure 4. Numbers of described taxa per indicated political or geographic entity in the New World; maps based on Fig. 1.

The Australasian and Pacific area of distribution generally received attention much later. More than 50% of the taxa were described in the second interval of discovery. Only 32% had been named before 1880 while at the same time in the New World 63% of the names were created. The earliest descriptions focused on Polynesian islands and the adjacent Fiji and Vanuatu archipelagos with exception of the Hawaiian Islands. A smaller share of New Caledonian, Australian taxa and of those from the coastal areas and islands of the Indian Ocean were described early as well. The second phase is characterized by the recognition of most of the helicinid diversity of Japan, continental Asia, the Philippines, Indonesia, Papua New Guinea and the Solomons. Most recent publications concentrate on the Ogasawara Islands of Japan (mainly Minato 1980), Australia (Stanisic *et al.* 2010), New Caledonia (Richling 2009), and far eastern Polynesian islands (Preece 1998, Richling and Bouchet 2013).

In the comparatively poorly-studied helicinids it is unlikely that the majority of regions—and more so tropical areas—are entirely explored for new species. In general, the

absence of any newly described taxa for certain areas points to a lack of serious, more recent studies and marks potential for still unrecognized diversity. This is certainly true for Mexico, Brazil, etc. in the New World and proven for the Lesser Antilles as an area with a long research history (see below). On the other hand, these areas are more likely to be over-described with a certain percentage of names disappearing into synonymy (see below). In more recently explored countries it is likely that the species accumulation curve did not yet reach the saturation zone, because late exploration also implies complex natural settings with still undiscovered diversity, *e.g.*, known for Costa Rica, see below, otherwise likely for parts of South America, Hispaniola and most of the Australasian and Pacific area where suitable habitat is left.

Described diversity versus “true” diversity

In the following section, selected case studies will be reviewed for the relation of described diversity to previously unknown species and the specific circumstances. A numeric summary is given in Table 1.

Costa Rica

Prior to the 1990's the Costa Rican species were poorly sampled and in need of revision. Richling (2004a) based her revision on extensive own field work and the mollusc collection of the Instituto Nacional de Biodiversidad de Costa Rica (INBio) with a good representation of recent material. The study combined morphological characters with distribution patterns and followed a rather conservative approach on the continuum of lumping to splitting. Out of 19 available names, eight species and one subspecies were accepted as valid. Seven new species and two new subspecies were described. Five taxa reported for the country were misidentifications of extralimital species. In general, species ranges turned out to be more restricted than previously assumed.

Remote regions of the remaining wooded areas of Costa Rica still have to be regarded as poorly explored and micro-molluscs (smaller than 3-4 mm) are insufficiently covered. Ongoing field work of this author revealed at least two more species of small-sized helicinids that await description.

Cuba

Clench and Jacobson (1968, 1971a, b) and Boss and Jacobson (1973, 1974) revised major groups of the Cuban helicinids (*Viana* H. and A. Adams, 1856; *Emoda* H. and A. Adams, 1856; *Glyptemoda* Clench and Aguayo, 1950; *Calidviana* Baker, 1954; *Ustronia* A. J. Wagner, 1908; *Troschelviana* Baker, 1922;

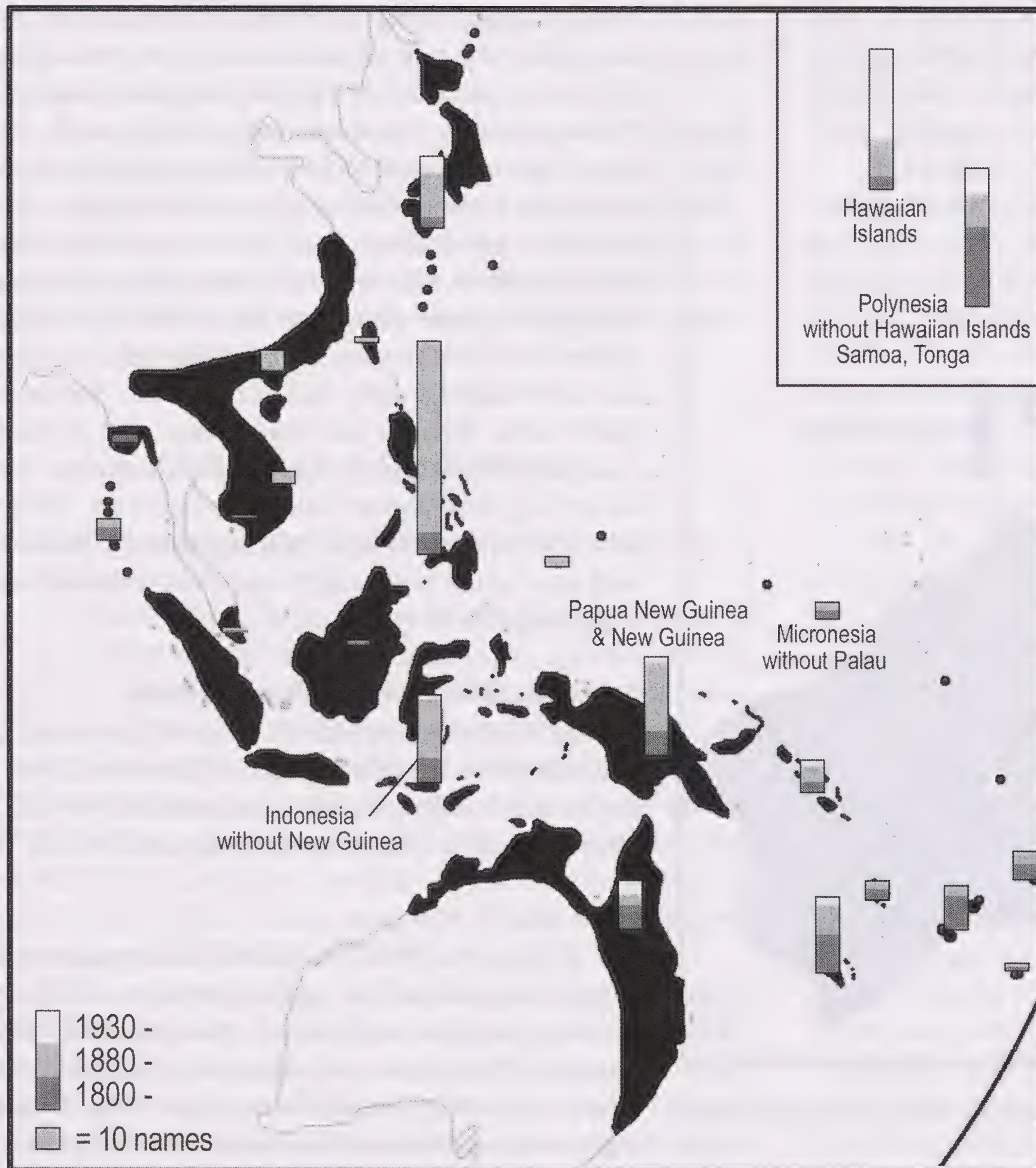


Figure 5. Numbers of described taxa per indicated political or geographic entity in the Australasian and Pacific area, Hawaiian and most of the Polynesian islands not in true geographical position; maps based on Fig. 1.

Semitrochatella Aguayo and Jaume, 1958; *Alcadia* Gray, 1840, and *Lucidella* Swainson, 1840). They accepted 61 species and 10 subspecies out of 150 names available and described one new species and two subspecies. Unlike the majority of other countries Cuba has a long tradition in field malacology starting with the remarkable explorations by the German Johann Christoph Gundlach, whose land snail collections were mainly investigated and described by L. Pfeiffer (Richling and Glaubrecht 2008). After the major revisions mentioned above only one additional helicininid species was described to date (Sarasúa 1976).

Jamaica

The Jamaican land snail fauna is currently being studied by Rosenberg and collaborators who undertook major collection

efforts between 1999 and 2002 with 607 major sites throughout the island (Rosenberg 2005, unpubl.). Jamaican helicininids were first intensely studied by C. B. Adams (mainly 1849, 1850a–c), followed by localized, but “incidental” collections by Baker (1934 a, b). According to the on-line published working list by Rosenberg and Muratov (2005, unpubl.), 40 species and 13 subspecies of helicininids other than Stoastomatinae are recognized out of 74 names. For the latter subfamily—treated as Stoastomatidae by the authors—75 species and one subspecies are accepted out of 82 available names. Because the Stoastomatinae underwent such an outstanding radiation only on Jamaica and, therefore, represent a special case, they are excluded from further calculations of diversity estimates.

Lesser Antilles

The Lesser Antilles represent a previously rather poorly sampled area that was never studied entirely because of the different political affiliations. Revisionary work on the helicininids is still in progress (Richling 2005b), but the unpublished data suggest that 23 species are valid out of 42 names available and four species await description.

Biogeographic relationships are still poorly understood and the application of new systematic concepts (Richling 2004a) reveals different distribution patterns of more closely related groups

than previously assumed. Some taxa currently regarded as single species occur on different islands while others represent island endemics characterized by distinct shell morphology. While for the latter recognition at the species level is fairly certain, the more widely spread taxa could equally comprise “cryptic” species that for unknown reasons did not diverge recognizably in morphology and would add to the helicininid diversity in the Lesser Antilles. These questions require molecular analyses.

New Caledonia

Although Franc (1957) and Solem (1961) provided compilations on the terrestrial snail fauna of New Caledonia, both authors only more or less critically summarized the helicininid species reported for the area. Richling (2009) provided the

Table 1. Previously known and unknown helicininid diversity after revisionary work for different areas compared to the number of available names and records for the area regardless of rank. For data sources and the additions for NE-Australia see respective paragraphs. n. = new, sp. = species, ssp. = subspecies.

Area	Number of available names	In respective revision, number of				Percentage of			
		accepted sp.	accepted ssp.	n. sp.	n. ssp.	valid sp.	valid sp. + ssp.	n. sp.	n. sp. + n. ssp.
New World									
Costa Rica	19	8	1	7	2	42.1	47.4	46.7	50.0
Cuba	150	61	10	1	2	40.7	47.3	1.6	4.1
Jamaica	74	40	13	?	?	54.1	71.6	?	?
Lesser Antilles	42	23		4		54.8	54.8	14.8	14.8
<i>Average</i>						<i>47.9</i>	<i>55.3</i>	<i>21.0</i>	<i>23.0</i>
Australasian-Pacific									
New Caledonia	31	14		3		45.2	45.2	17.6	17.6
NE-Australia	11+6	6+1		6-1		41.2	41.2	41.7	41.7
Hawaiian Islands	27	10	9	6	34	37.0	70.4	37.5	67.8
Gambier Islands	2	1		9		50.0	50.0	90.0	90.0
<i>Average</i>						<i>43.4</i>	<i>51.7</i>	<i>46.7</i>	<i>54.3</i>
Total Average						45.6	53.5	35.7	40.9
Central America	116	70	23			60.3	80.2	65.0	65.0

first true revision of the New Caledonian helicininids and also the first contribution based on a significant amount of material (460 lots from over 260 stations) collected throughout the islands mainly by Philippe Bouchet and Simon Tillier in the late 1970’s and 1980’s. Fourteen species were accepted out of 31 available names and only three species previously not recognized. One taxon was considered as misidentification of a species occurring somewhere else which is not surprising for an isolated island setting with endemic species.

An amazing conchological convergence of the two most widely spread species on Grande Terre and adjacent islands combined with high intraspecific variability constitute the main reasons for half of the synonyms that were created despite the inadequate recognition and description of consistent differentiating characters. Two of the new species are local endemics and were absent in all old collection material revised.

The study applied a conservative approach, but it is suspected that a few “species” may involve species complexes that could not be resolved with morphological methodology and the material available. Molecular analyses were impossible due to inadequate conservation of the collections.

Northeast Australia

Stanisic in Stanisic *et al.* (2010) described six new species from northeast Australia, thus, implying that this can be regarded as a revision although the presentation is very condensed within this huge opus. Six species were accepted out

of eleven previously described taxa listed by Stanisic *et al.* (2010). Another four species described from Australia (*suprafasciata* Sowerby, 1874, *zebriolata* Pfeiffer, 1865, *fulgurata* Cox, 1865, and *crassidens* Tate, 1899) were recognized as extralimital taxa by previous authors (*e.g.*, Iredale 1937). Stanisic *et al.* (2010) did not mention the obviously true East-Australian taxa *turbinella* Pfeiffer, 1855 and *yorkensis* Pfeiffer, 1862 which, have the potential to represent an older name for one of the new species from New South Wales (*turbinella*) and a synonym of *gouldiana* Forbes, 1851 (*yorkensis*). These six taxa were included in the count in table 1 in the outlined sense. Other Australian taxa occur outside the study area of Stanisic *et al.* (2010).

Hawaiian Islands

Neal (1934) provided a detailed analysis of the helicininids of the Hawaiian Islands based on extensive field collections and building on the previous, but less comprehensive study by Pilsbry and Cooke (1908). She accepted ten species and nine subspecies out of 27 taxa previously mentioned for the islands, six taxa were identified as erroneous records of species occurring elsewhere. Neal added six new species and 34 “varieties”, adapting the idea of differentiating restricted local forms as was practice in other Hawaiian land snails groups with the most well-known genera *Achatinella* Reeve, 1850 and *Partulina* L. Pfeiffer, 1854. A formal, rather nomenclatural update by Richling (2011), including the study of types, presented a number of species and subspecific units in a similar range.

It is undoubted that the extreme isolation of the Hawaiian islands combined with a particularly rough topography and climate favored a high rate of endemism, but it remains to be investigated with modern approaches which taxonomic rank is appropriate or, applying terms of evolution, how much divergence the numerous subspecific units will show as such and in a larger frame. Initial molecular data were obtained from the very few surviving species by Leung *et al.* (2013) and the authors suspect cryptic species among the described varieties.

Gambier Islands

The most recent contribution on an island helicininid fauna revealed a previously largely unknown radiation on the small archipelago of the Gambier Islands located at the eastern out-reaches of the Polynesian islands with a total diversity of ten species, of which only one was previously described and another species was erroneously reported for the archipelago (Richling and Bouchet 2013). This high diversity with up to eight species on a single island is outstanding for small Pacific islands, *e.g.*, the larger Henderson Island in the Pitcairn group was inhabited by only three species (Preece 1998).

Estimating diversity

The percentage of valid species in the eight studies analyzed ranged from 37 to 54.8% with an average of 45.6% (Table 1). When considering a splitting concept, which is here approached by accepting subspecies as units of diversity, this average climbs to 51.7% with a range from 41.2 to 71.6%. This means that about half of the number of taxa described or

more fall into synonymy. On the other hand, after a rigorous revision (seven studies) 35.7% of the accepted taxa represent previously unknown diversity with only 1.6% in a well-studied area such as Cuba and up to 90% on the Gambier Islands. Applying the same splitting approach the newly described taxa constitute 40.9% with a range from 4.1% to 90%.

Thompson’s (2011) catalogue of the Central American land and freshwater snails undoubtedly covers the largest area treated by a well-founded compilation including helicininids. Although it does not focus on revisions, it provides an estimate of diversity. Thompson accepted well-established synonyms and as a principle treated all taxa described below species level as subspecies. With these criteria he lists 70 valid species and 23 subspecies out of 116 available names (Table 1). His percentage of valid species is with 60–80% significantly above average, which is to be expected in a non-revisionary approach. For all land and freshwater snail families Thompson (2011) estimated that only about 35% of the diversity is known. He based his assessment on over half a century field experience throughout Central America, the diverse natural settings and the coverage in past explorations. Sixty-five percent of new taxa is a value clearly above the helicininid average and also higher than in Costa Rica which was once one of the most-poorly studied countries in Central America. If Thompson’s estimate and the present considerations prove correct, helicininids would be among the better documented land snail families in Central America.

Comparing the number of valid taxa to the taxa described for a global estimate, 62% represent the “true” diversity in a rather conservative approach and 112% in the more splitting concept (Table 2). The Gambier Islands case, however,

Table 2. Recognized helicininid diversity after revisionary work for different areas compared to the number of available names and records for the area regardless of rank. For data sources see respective paragraphs. Numbers in parentheses also calculate the taxa from the Gambier Islands.

Area	Number of available names	In respective revision, number of valid taxa		Percentage of resulting recognized diversity	
		species	including subspecies	species	including subspecies
New World					
Costa Rica	19	15	18	78.9	94.7
Cuba	150	62	74	41.3	49.3
Jamaica	74	40+?	53+?		
Lesser Antilles	42	27	27	64.3	64.3
<i>Average</i>				<i>61.5</i>	<i>69.5</i>
Australasian–Pacific					
New Caledonia	31	17	17	54.8	54.8
NE-Australia	17	12	12	70.6	70.6
Hawaiian Islands	27	16	57	59.3	211.1
(Gambier Islands)	2	10	10	(500)	(500)
<i>Average (incl. Gambier)</i>				<i>61.6 (171.2)</i>	<i>112.1 (209.1)</i>
Total average (incl. Gambier)				61.5 (124.2)	90.8 (149.3)

appears abnormal in the small dataset. Considering the six other case studies are roughly representative for the whole area of distribution, the helicininid diversity would range from 770 to 1,140 species or up to 1,400 species if the studies from the Australasian-Pacific area are more typical.

Drawbacks in exploration

Helicininids meet a number of criteria that should make them favorites for researchers such as a size that makes them easy to work with, a comparatively high abundance among the larger land snail fauna in many areas, and—not to be ignored—their often colorful appearance. Despite these advantages and as shown above, even smaller local revisions of the family were not often attempted for the following possible reasons:

Questionable systematic concepts above species level

Until quite recently, higher systematics for the majority of helicininids, namely representatives of the genera *Helicina* Lamarck, 1799 and *Alcadia sensu* Wagner (1907–1911) and almost all Australasian and Pacific species, were based entirely on shell shape and opercular characteristics. The generic concept proposed by Wagner (1907–1911) was subsequently partially modified by seemingly applicable radular features (mainly Baker 1922a, but importance confirmed also by Bourne 1911), elaborated by the creation of new taxa and nomenclaturally corrected and adapted by the use of appropriate type species (Keen 1960), but essentially no other characters were incorporated. The major anatomical investigations by Bourne (1911) and Baker (1926, 1828) basically failed to find significant features and the value of radular characteristics was increasingly and rightfully questioned (Solem 1959, Boss and Jacobson 1973).

Thompson (1982) was the first to point to the importance of the embryonic shell structure and his detailed anatomical studies for the related families Proserpinidae and Proserpinellidae and systematic considerations greatly inspired subsequent research. Richling (2004a) evaluating characters of shell, radula, and anatomy for Central American taxa proved the applicability of features of the female reproductive system along with the embryonic shell structure as main distinguishing elements for Neotropical genera. Furthermore, doubts in radular features were confirmed and incongruity with Wagner's concept likewise revealed the shortcomings in opercular characteristics for the majority of genera. For more details and on the history of systematic concepts see Richling (2004a, 2009, 2011). The new hypotheses were further elaborated and applied to certain Pacific helicininids (Richling 2009, 2011), but a helicininid range-wide coverage as well as supporting molecular analyses are still in progress. Consequences for alpha-taxonomic work are further discussed in the next paragraph.

Limited recognized differentiating characters and convergence

While helicininids as family are clearly defined and easily recognized, differentiating shell characters on a lower systematic level are often missing. The majority of helicininids lacks the most directly accessible features like apertural barriers other than and because of the operculum, sophisticated breathing devices like other operculates, or obvious shell sculpture. Shell coloration and subtle differences in shell shape remain simple options. However both characters need to be used with great care and are often only meaningful when comprehensive collections of a given area and populations are available to evaluate the range of variation—a major weakness in many older descriptions. The operculum only rarely provides features for species delineation other than reflecting the shape of the aperture. Only some species of the genus *Eutrochatella* Fischer, 1885 in a very broad sense, of *Alcadia*, *Nesiocina superoperculata* Richling and Bouchet, 2013 (see also discussion in the species description) and the Stoastomatinae developed some unusual external structures on the operculum.

As in other snail families (e.g., Helicidae, Orthalicidae, Bulimulidae, Achatinellidae), bright coloration is an adaptation to an arboreal lifestyle and, therefore, subject to multiple convergences. In helicininids, Richling (2004b) observed that the coloration in live snails can be realized in two different ways: through the “usual” shell coloration or, the colorful mantle pigmentation that shines through the thin, transparent shell. It is assumed that the latter is linked to habitats with limited calcium carbonate availability. Additionally, it is suspected that the visible coloration in some species changes throughout ontogeny with juveniles (and small sized species) being rather dark (perhaps imitating feces as camouflage) and the adults brightly colored and mottled.

Up to now comparative studies failed to find significant species-specific differences in the genital system (e.g., Baker 1926, Richling 2004a, 2009) like those extensively described for several pulmonate families with little differentiation in external features and intergrading shell shapes (Lymnaeidae, Zonitidae, Oxychilidae, Succineidae, Hygromiidae, etc.). Therefore, shell shape still represents the most important morphological diagnostic feature on the level of alpha taxonomy for the Helicininidae. Circumstantial evidence suggests that, in fact, it constitutes a main driving force in helicininid speciation because more closely related species in a given area tend to diverge conchologically, *i.e.*, into different size classes, shapes, occasionally also connected with a different lifestyle like arboreal or ground-dwelling (Fig. 6 with examples for Costa Rican species of *Helicina* and New Caledonian species of *Sturanya* A. J. Wagner, 1905). However, independent evidence, e.g., genetic characters, are still needed to avoid a circular argument. The only substantial molecular analysis of helicininids so far investigates geographically structured

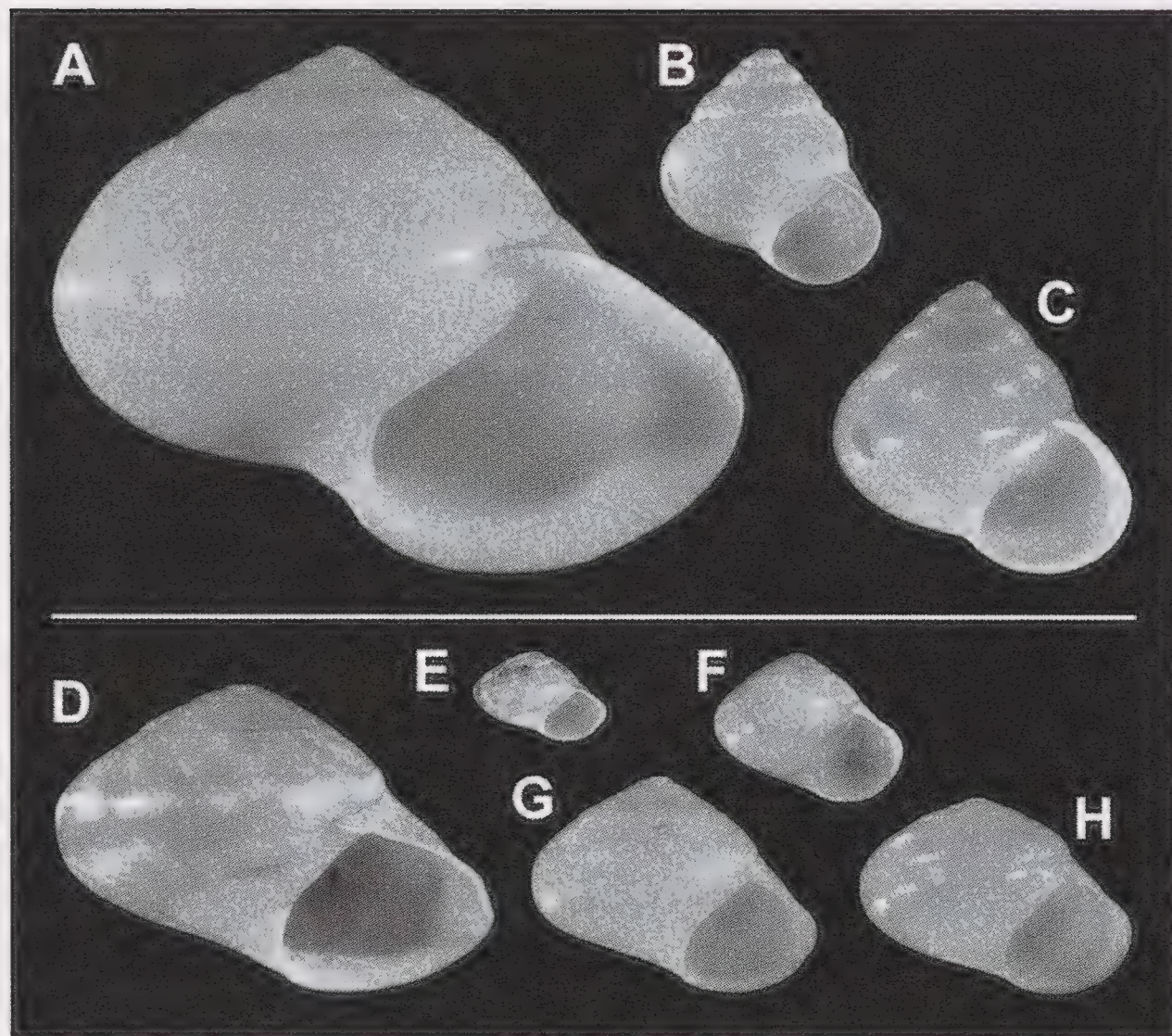


Figure 6. Typical co-occurrence of related helicimid species with different conchology. **Upper panel.** Species of the genus *Helicina* in the area of Río Barbilla, Costa Rica: **A**, *Helicina funcki*, **B**, *H. chiquitica* (Richling, 2001), **C**, *H. escondida* Richling, 2004, **Lower panel.** Species of the southern radiation of *Sturanya* on Mt. Mou, Grande Terre, New Caledonia: **D**, *Sturanya laeta* (Crosse, 1870), **E**, *S. littoralis* (Mountrouzier, 1859), **F**, *S. mouensis* (Crosse, 1870), **G**, *S. macgillivrayi* (L. Pfeiffer, 1855), **H**, *S. benigna* (Crosse, 1870) (ground-dwelling?). All at same scale.

subspecific taxa of *Viana regina* (Morelet, 1849) in Cuba. Preliminary results suggest that the conchological differentiation reflects phylogenetic relations rather than an ecophenotypic background (Herrera *et al.* 2013).

Most confusing patterns regarding shell shape occur when species of different phylogenetic entities are involved. Obviously, the evolutionary potential of the helicimid shell shape is rather limited, which is reflected in the observations above on limited characters, so that within different groups often similar morphologies have evolved. Against the background of partially still poorly understood higher systematics within the helicimids, this complicates alpha taxonomy. The most amazing example of such shell convergence I experienced was with the most widely spread and above mentioned New Caledonian species *Sturanya macgillivrayi* (L. Pfeiffer, 1855) and *S. novaecaledoniae* (Baird, 1873) which can only be reliably differentiated by microstructural differences of the teleoconch surface and postembryonic shell (Fig. 7), both features were found to characterize two also geographically structured radiations (Richling 2009). Nearly ten synonyms were created and no concept about the species' distribution existed before these characters were recognized.

Species complexes

The question of possible “cryptic” species within species complexes was brought up in the case study of the Lesser Antillean species, but equally applies to other areas with truly isolated populations of high conchological similarity usually combined with a high variability within the populations. The small, depressed, often angulated to carinated so-called “*Pleuropoma*”-species with a flame pattern that occur throughout parts of the southern Pacific (*e.g.*, on islands of New Caledonia, Vanuatu, Fiji, Samoa, Tonga, etc. encompassing taxa like *gallina* Gassies, 1870, *articulata* L. Pfeiffer, 1853, *vitiana* Mousson, 1870, *vitiensis* Mousson, 1865, *diminuta* Mousson, 1871, *subcarinata* Mousson, 1870) certainly represent a prime example. Adding to the conceptual difficulty, taxa were occasionally described with multiple type localities or with uncertain origin.

Here, traditional methodology approaches its limits and molecular case studies are urgently needed. Dispersal capability is one of the key questions and probably the least understood. However, this goes far beyond the difficulties in understanding specifically helicimid diversity and, thus, the scope of this paper.

Limited wet preserved material

As mentioned above, anatomical features revealed only limited applicability on species level differentiation, but proved invaluable for generic assignment (Richling 2004a, 2009) which is often impossible by shell characters alone. But even on species level simple information like the sex in this dioecious family can be substantial because of groups with a significant sexual dimorphism, *e.g.*, “*Gemma*”-group of the Costa Rican species (Richling 2004a). Radula features allow conclusions on the lifestyle (*e.g.*, substrate preference) in absence of field observations. The need of ideally fresh and water-free preserved tissue samples for molecular analyses is obvious.

Personal observations show that only few museum collections have significant holdings of ethanol preserved helicimid material which is most likely explained by the tropical center of distribution. In early times there was no tradition for wet collections and in more recent times, growing legal restrictions seriously hamper diversity documentation and, thus, collections in the tropics. Furthermore, the habitat of this mostly forest-dwelling group is disappearing at dramatic rates rendering collections increasingly difficult to impossible when species already went extinct (see below).

Another practical drawback, if material was preserved, concerns the specific and deviating anatomy of helicimids when compared to other land snails. When bodies and shells were routinely separated to ensure better preservation especially in operculate species, important anatomical features were often irreversibly destroyed. In the majority

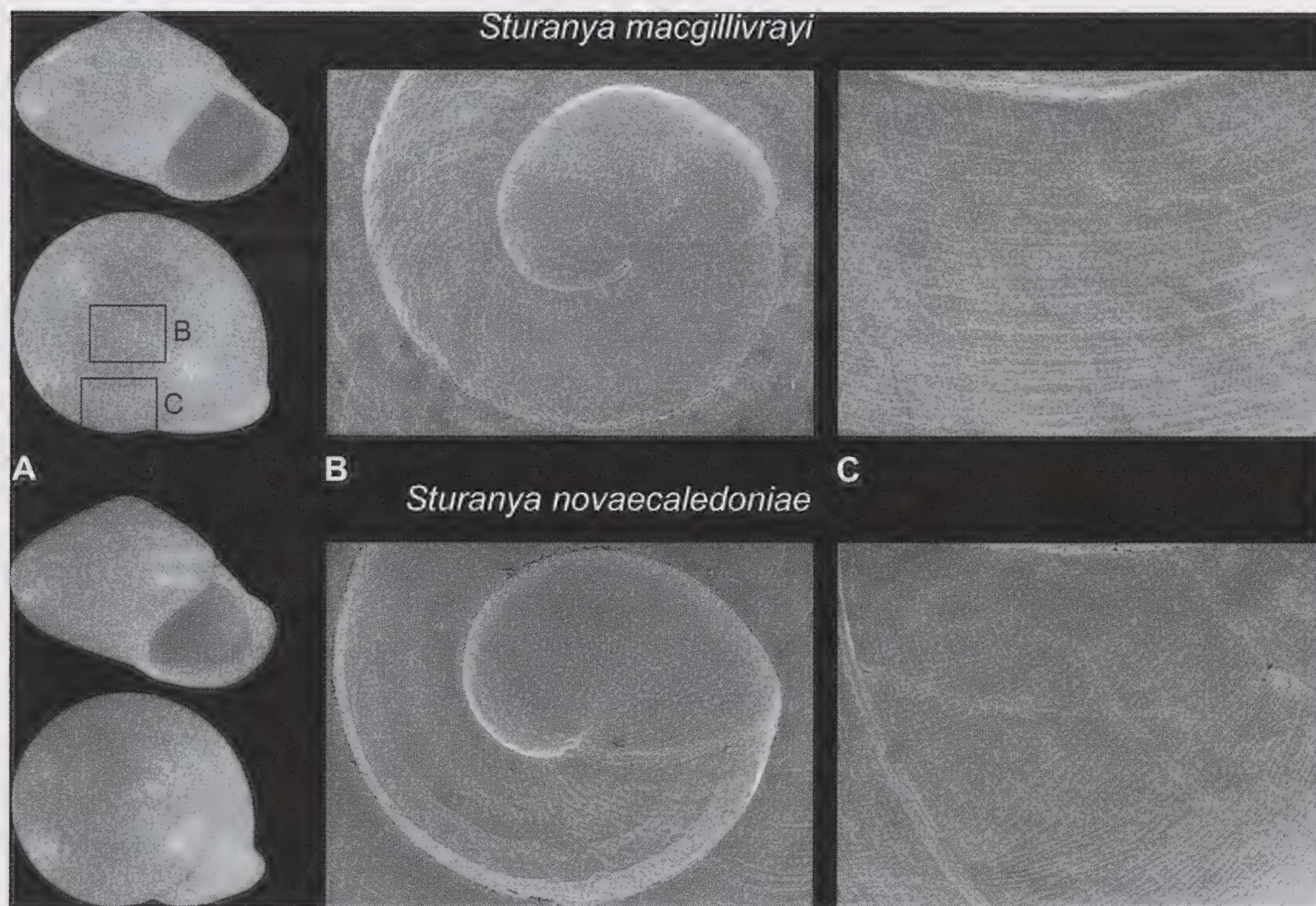


Figure 7. Convergence in the New Caledonian helicínids *Sturanya macgillivrayi* and *S. novaecaledoniae*; **A**, shell shape, **B**, surface structure on early postembryonic whorl with numerous fine parallel spiral lines in *S. macgillivrayi* and only 2–3 strong spiral ridges in *S. novaecaledoniae*, **C**, surface structure on later teleoconch with parallel lines in *S. macgillivrayi* and oblique diverging grooves in *S. novaecaledoniae*.

of pulmonates the distal part of the body and almost always the important part of the genitalia will be kept in good condition even if the body breaks whereas in helicínids the posterior pallial gonoduct with the systematically relevant and often very fragile structures will be ruptured and, thus, destroyed. The relevant parts would remain inside the shell and, thus, have been dried. The most frustrating example I have seen were different lots of *Sturanya uberta* (Gould, 1847) from O'ahu, Hawaiian Islands with numerous specimens in each lot but of which only 1–2% still possessed the required anatomical parts. These samples may represent the only preserved material of this extinct species and type species of *Orobophana* A. J. Wagner, 1905. Therefore, preserved helicínids should be kept with their shells when being prepared by people not familiar with the special body shape of helicínids. Finally, separate sexes cause another difficulty in that statistically twice the amount of material is required to be likely to have a female with the important structures.

Massive habitat loss, increasingly fragmented distribution, and extinction

While for a large share of helicínids, especially in the Australasian and Pacific region, populations/species are isolated *per se* by the colonization of or survival on archipelagos and islands, in other areas human impact fragments distribution

ranges. The knowledge of the habitat requirements of helicínids is rather limited to singular observations or general statements without detailed ecological analyses. These and personal observations indicate that most species are restricted to “wet” forest habitats. They range from coastal and moist to cloud forests with decreasing humidity as limiting factor of distribution. In Costa Rica Richling (2004a) observed that the most ecologically tolerant species, *Helicina tenuis* L. Pfeiffer, 1849, is absent in areas with dry forest (vegetation type after map by Tosi 1969) and less than 2,000 mm precipitation/year in regions with a marked dry season. In areas of less seasonally contrasting climatic conditions with higher humidity throughout the year the threshold of rainfall might be lower. In southern Veracruz, Mexico the same species was even observed in savannah forests (Baker 1922b). However, the ecological span of *H. tenuis* is rather outstanding and most other species have much more restricted

distribution ranges and habitat requirements. While for Costa Rica Richling (2004a) reported several species also from secondary growth (rather shrubs) and even cultivated areas (*Helicina funcki* L. Pfeiffer, 1849, *H. pitaleensis* A. J. Wagner, 1910, *H. beatrix beatrix* Angas, 1879, *H. b. confusa* (A. J. Wagner, 1908)), in these places remains of forests were still in the closer proximity or deforestation was not complete like in smaller hand-tended plantations under remaining trees (as found in remote, rural places of poor people). The other eight species of Costa Rican *Helicina* and *Alcadia* were so far only reported from natural forests.

In the middle of the last century massive deforestation started in the small Central American country with an original forest cover of about 90%. In 1984 Sader and Joyce (1988) calculated 17% remaining forest whereas a more recent analysis in 1991 with higher resolution resulted in 29%, but with increased fragmentation (Sánchez-Azofeifa *et al.* 2001). Tropical and premontane moist forest was almost completely eliminated by then and in vast areas only small disconnected patches were left over as remaining habitat for helicínids. The consequences for systematic studies are obvious: 1) field sampling can only result in equally or usually way more fragmentary records for a given species; 2) taxon/population sampling for different kinds of analyses will be rather chance driven than by scientific questions; 3) intergrading populations or sympatric occurrences of species—both important patterns

to understand species delineation—will often be erased; and 4) populations at type localities, especially of older descriptions, are often wiped out. A good example (with the exception of number 4) is given by *Helicina beatrix*, its subspecies, and their possible relation to *Helicina gemma* Preston, 1903 (for maps and details see Richling 2004a); molecular studies are still pending.

A much more dramatic picture is found on many Pacific islands. My own fieldwork on the 78 km²-sized Uvea island (belonging to the French overseas collectivity “Territory of the Wallis and Futuna Islands”) in the Pacific during an invasive species survey (Meyer *et al.* 2008) recovered populations of two previously reported (Mousson 1871) species of heliciniids. However both species very strictly limited to the very few remaining patches of native or fragmentary native forest on this strongly anthropogenically altered island. While the arboreal *Sturanya ueana* (Mousson, 1871) still occurred in seven of such isolated places, the second more ground associated species was found alive only in an area of less than one hectare. Although not as severely threatened as other tropical land snail families such as Endodontidae, Partulidae and Achatinellidae, the demise of heliciniids on certain Pacific islands seems definite. A significant amount of taxa of the Hawaiian Islands obviously went extinct (Solem 1990, Leung *et al.* 2013) and only recently Richling and Bouchet (2013) described the heliciniids of the Gambier Islands documenting the extinction of nine, mostly previously undescribed species representing 90% of the heliciniid diversity. In this special case, the extinctions not only hampered our understanding of alpha-diversity by restricting the methodology to shell characters only, but at the same time on the generic level and for evolutionary processes, because the Gambier heliciniids developed several shell characters unique for all Pacific species of the family. The current state of knowledge does not allow a well-founded generic assignment without an anatomical or potentially molecular analysis (Richling and Bouchet 2013).

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